

A comparison of mortality rates between top height trees and average site trees

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Abstract

- Although comparisons between methods of selecting trees for site index estimates are well documented in the literature, little is known on mortality rates of different canopy tree cohorts used for that purpose.
- This study was initiated to test the hypothesis that the mortality rates of top height trees are lower than those of codominants only or a combination of codominant and dominant trees. To test this hypothesis, we used records from a network of permanent sample plots in Québec and studied the fate of different cohorts of site trees for five different species.
- Our results did not show clear evidence of lower mortality rates for top height trees. Instead we found that depending on the species, top height trees have lower (*Populus tremuloides*, *Pinus banksiana*), higher (*Picea mariana*, *Abies balsamea*) or equal mortality rates (*Betula papyrifera*) than codominant trees or codominant and dominant trees combined.
- These results suggest a tendency for shade intolerant species to maintain lower top height tree mortality rates over time when compared to shade tolerant species. In the latter case, it is also shown that spruce budworm epidemics (*Choristoneura fumiferana*) did not change the pattern of mortality rates of site trees of *A. balsamea*.

Mots-clés :

hauteur dominante /
arbres indicateurs de la station /
taux de mortalité /
indice de qualité de station /
placette-échantillon permanente

Résumé – Étude comparative des taux de mortalité entre les arbres dominants et les arbres indicateurs moyens de la station.

- Bien que des études comparatives sur les méthodes servant à déterminer l'indice de qualité de station sont disponibles dans la littérature, on connaît peu de choses sur les taux de mortalité des différentes cohortes d'arbres utilisées à cette fin.
- Cette étude a été initiée dans le but de tester l'hypothèse selon laquelle les taux de mortalité des arbres dominants sont plus faibles que ceux des arbres codominants ou de ceux d'une combinaison d'arbres codominants et dominants. Afin de tester cette hypothèse, nous avons utilisé la base de données des placettes-échantillons permanentes du Québec et nous avons suivi la destinée de différentes cohortes d'arbres indicateurs de la station pour cinq espèces différentes.
- Nos résultats n'ont pas montré de façon tranchée que les arbres dominants ont un taux de mortalité inférieur à celui des autres cohortes à l'étude. Nos résultats démontrent plutôt que selon les espèces, les arbres dominants ont un taux de mortalité inférieur (*Populus tremuloides*, *Pinus banksiana*), supérieur (*Picea mariana*, *Abies balsamea*) ou égal (*Betula papyrifera*) au taux de mortalité des arbres codominants ou à une combinaison d'arbres codominants ou dominants.
- Ces résultats suggèrent que les taux de mortalité des espèces classées intolérantes à l'ombre ont tendance à demeurer plus faibles dans le temps lorsqu'on les compare aux taux de mortalité des espèces tolérantes à l'ombre. Pour ces dernières, les résultats démontrent de plus que l'effet des épidémies de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana*) n'ont eu aucun effet sur les patrons de mortalité des différentes cohortes d'arbres indicateurs de la station en ce qui concerne *A. balsamea*.

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1. INTRODUCTION

Foresters have long been interested in ways of interpreting and classifying the growth potential of trees in areas of varying site quality. Early observations of height growth differences between trees of the same species growing on different soils date back to the second half of the 18th century in Germany and France (Batho and Garcia, 2006; Skovsgaard and Vanclay, 2007). These works inspired in turn the development of site index curves in Germany in the 19th century and a few decades later the concept of site index spread to Scandinavia and to the United States (Cajander, 1926; Jones, 1969; Hägglund, 1981 for a review).

Site index has been defined as “forest site quality based on the height, at a specified age, of dominant and codominant trees in a stand” (Haddon 1988). In the province of Québec for instance, site index has generally been estimated using a combination of codominant and dominant site trees (*Ministère des Ressources naturelles du Québec*, 2001). Although trees belonging to these cohorts were commonly used in the past, site index is nowadays based on the height of selected dominant trees, for example the 100 largest trees per hectare (Curtis and Marshall, 2005), at a reference age of 50 years taken at breast height, and these trees are generally referred to as “top height trees” (Garcia and Batho, 2005).

The use of dominant trees for estimating site quality is not new. For instance, as early as 1880 in Germany dominant height was computed as the mean height of the largest (by diameter at breast height) 20% of the trees on a plot (Weise, 1880, cited by Sterba and Amateis, 1998). Later, Schwappach (1893, cited in Zeide and Zakrzewski, 1993) proposed to use 100 largest diameter trees per hectare. To a large degree, there are many advantages of using top height trees: they are easier and faster to measure (Staebler, 1948), they have larger crowns and thus a higher probability of survival than do the tallest trees (Zeide and Zakrzewski, 1993) and estimates of dominant height have been found to be more precise than those based on dominant and codominant trees combined (Carmean, 1975; Dahms, 1966; Ker, 1952). Also, dominant trees are less variable in height than are dominants and codominants combined, and therefore fewer dominant trees are needed to attain a specified level of accuracy (e.g. Ker, 1952). Finally, in even-aged stands the height of the largest trees is relatively independent of stand density (Skovsgaard and Vanclay, 2007) which makes it an effective indicator of site productivity.

As much as dominant trees are preferable for site index determination, there are some disadvantages of using them too. Selecting proper site trees is essential to avoid biasing the estimated site index (Nigh and Love, 1999), but this can sometimes be difficult owing to the risks associated with top damage of the upper canopy trees that can occur due to climatic or pest events. Also, care must be taken when determining plot size since it can affect estimates of top height and corresponding estimates of site index (Garcia, 1998; Magnussen, 1999). Another potential problem is that the status of dominants may change over time, a phenomenon associated with the concept of rise and fall in social ranking (Assmann, 1970) or dominance switching (Feng et al., 2006). The latter observa-

tion raises the question of stability of dominance and mortality rates of top height trees in a forest stand in relation with site quality estimates, although this may be true for average site trees as well (e.g. codominants and dominants combined).

Even though comparisons between methods of selecting trees for site index estimates are well documented in the literature (e.g. Ker, 1952; Dahms, 1966; Mailly et al., 2004), little is known on mortality rates of different canopy tree cohorts that are best suited for site index estimation. Moreover, because site index curves are often adjusted using top height and age data from repeated measurements of permanent sample plots, it is important to consider the fate of trees used for that purpose. To address these questions we initiated this study which aims at testing the hypothesis that the mortality rate of top height trees is lower than the mortality rate of codominants only or a combination of codominant and dominant trees. This hypothesis will be tested using permanent sample plot data covering species of different shade tolerances growing in the province of Québec.

2. MATERIALS AND METHODS

2.1. Data

Data for this study come from permanent sample plots that are part of a network that was initiated in the early 1970's by the *Ministère des Ressources naturelles et de la faune du Québec*. Its original purpose is to acquire and diffuse information on the state of forest ecosystems in the province of Québec. The network comprises over 12000 plots from various sources which are spread over seven bioclimatic domains (Robitaille and Saucier, 1998). The information collected in such inventory plots are used by forest managers in the preparation of management plans. It is also used in the calibration of forest simulation models and in providing valuable information for the calculation of annual allowable cuts.

Each plot in the network is circular, 400 m² in size with a 11.28 m radius, and is remeasured every ten years on average. Within each plot, trees whose diameter at breast height (i.e. 130 cm, D₁₃₀) is greater than 9.0 cm are considered merchantable and are tallied (*Ministère des Ressources naturelles du Québec*, 2001). Saplings taller than 130 cm but with a D₁₃₀ smaller than 9.1 cm) are considered unmerchantable trees and are tallied by 2-cm D₁₃₀ classes within a 40 m² subplot centered in the main plot. Nine site trees per plot are sampled for height and age determination (ring count taken at 100 cm aboveground). Four site trees among these are called “representative trees” and are chosen based on three selection criteria: they must be located close to the plot center, must have a D₁₃₀ close to the average D₁₃₀ of codominant and dominant trees and must belong to the codominant or dominant canopy class. The remaining five trees, called “systematic trees”, are systematically chosen based on their rank, which is determined by dividing the total number of merchantable trees by five, and by multiplying the quotient by 1, 2, 3, 4 and 5 to attribute a tag number to the tree.

2.2. Analysis approach

Five species of difference shade tolerances were selected for this study (in ascending order of shade tolerance): trembling aspen

(*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.), white birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* (Mill.) BSP), and balsam fir (*Abies balsamea* (L.) Mill.). Permanent sample plots (PSP) dominated by these species had to satisfy the following criteria: (i) having less than 75% of estimated mortality (ocular estimation during inventory) due to the spruce budworm [*Choristoneura fumiferana* (Clem.)] (if over 75%, the current and the following measurements are withdrawn from the dataset), fire, blowdown, dieback and ice damage; (ii) have not been silviculturally treated or disturbed, and (iii) composed of at least 50% of merchantable basal area of the target species at the first measurement. In order to be candidates for selection, trees had to satisfy the following criteria: belonging to the codominant or dominant class, being of the target species, and being alive and healthy (state code 10 and 12, see Appendix). In addition, plots were selected if the average age of site trees for each species fell within a range considered adequate for site index estimation (Shongming Huang, pers. comm.). The minimum age was set to 20 years (Jones, 1969) whereas the maximum age was determined based on the age distribution and the longevity of the species. This resulted in maximum ages of 100 years for trembling aspen, 120 years for jack pine and white birch, 140 years for white spruce and balsam fir and 180 years for black spruce.

In order to eliminate the effect of the mortality due to the spruce budworm for black spruce and balsam fir trees, further restrictions to the data set were applied for building a subset of data. The elimination of PSP affected by the spruce budworm was achieved using the following procedure. Firstly, all PSP that had between 25 and 75% of estimated mortality (ocular estimation during inventory) due to the spruce budworm were withdrawn from the dataset. Secondly, any PSP that could be associated with a period of defoliation as estimated by photointerpretation was also withdrawn from the dataset as well as the following measurements of the same PSP. Such defoliation reports are conducted annually by the Conservation Branch of the *Ministère des Ressources naturelles et de la faune* (Québec) and cover the entire geographical distribution zone of balsam fir. The presence/absence of tree defoliation is estimated on areas covering 60 km² on average and each PSP is associated with such areas.

Three different site tree selection methods were used in this study. The first method consisted in selecting the four largest diameter (D_{130}) trees of the same species per 0.04 ha circular plot (cf. Forest Productivity Council of British Columbia, 1998) for trees of crown class D (dominant) or C (codominant). This method will be referred to the top height tree “4+” method throughout the text. The second method consisted in randomly selecting four site trees of the same species per 0.04 ha circular plot among those belonging to the codominant cohort. The method will be referred to the “C” method throughout the text. The third method consisted in randomly selecting four site trees of the same species per 0.04 ha circular plot among those belonging to the dominant or codominant cohort. The method will be referred to the “CD” method throughout the text.

Additionally, the following plot selection criteria were applied according to the different methods when applicable: (i) for method 4+, sample plots which had site trees having a D_{130} span greater than 20 cm were dropped from the database in order to exclude veterans; (ii) for methods C and CD, if there were more than 4 site trees satisfying the selection criteria, four trees were randomly selected per plot using PROC SURVEYSELECT (SAS Institute Inc., Cary, North Carolina, USA, version 9.1.3); (iii) for all sample plots, trees that were categorized as intruder (state code 25) or unidentified (state code 29) or joined (state code 29) were removed from the plot. Only PSP for

which all selection criteria were satisfied for the three methods were kept for the analyses.

2.3. Statistical analyses

A generalized linear mixed model was used to model the response variable (live or dead status of individual trees) following the re-measurement of PSP plots. The statistical model was fitted using the GLIMMIX procedure (SAS Institute Inc., Cary, North Carolina, USA) in order to take into account the hierarchical structure of the data, by the inclusion of random effects in the model. Indeed, trees in the same plot are likely to be correlated, trees observed in the same period for a plot and observations made on the same tree in a plot-method as well. A *cloglog* link was used and an *offset* variable corresponding to the log of time interval between two measurements was included in the model and its coefficient was set to 1 (Fortin et al., 2008; Rose et al., 2006). The general model considered for the five species of interest was:

$$\ln(-\ln(1 - \pi)) = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \ln(\Delta t)$$

where $\boldsymbol{\pi}$ is a vector with elements $\pi_{ijkl} = P(\mathbf{y}_{ijkl} = 1)$, the probability of mortality of tree k of method j , of plot i in period l , with (see Appendix):

$$y_{ijkl} = \begin{cases} 1, & \text{if state} = (14, 16, 23, 24, 34, 36, 44, 46, 54, 56) \text{ (dead tree)} \\ 0, & \text{if state} = (10, 12, 30, 32, 40, 42, 50, 52) \text{ (live tree)}. \end{cases}$$

\mathbf{X} is the design matrix of independent variables, $\boldsymbol{\beta}$ is a vector of unknown fixed-effect parameters associated with the independent variables and Δt is a vector whose elements are Δt_{ijkl} , the number of years of period l for tree k , of method j , of plot i . \mathbf{Z} is the design matrix of random effect and \mathbf{u} is the vector of the unobserved random effects. The three random effects considered are the plot, the period and the tree random effect.

The independent variable tested in the model is the site tree selection method (4+, C, CD). The basal area (BA) at the beginning of the period is also tested as a covariable for taking into account possible differences between the plots. The interaction between the selection method and BA is also included in the model. If the interaction between the two fixed effects (method and BA) is found to be significant ($\alpha = 0.05$), multiple comparisons are conducted between methods for three specific levels of merchantable basal area of the plot, i.e. Q1, median and Q3. When the interaction is not significant, it is withdrawn from the model and the three methods are compared between each other at the mean value of the merchantable basal area if the fixed effect “method” is significant. If BA is not significant, it is also withdrawn of the model.

Because the Hosmer and Lemeshow test statistic is very sensitive to the grouping choices (Hosmer et al., 1997), goodness of fits of model predictions were done using graphical evaluations of predicted values against observed data. In general, a good fit is achieved when the slope of the relationship is close to 1 and the intercept is close to zero (equation: $y = x$). Receiver operating characteristic curves (ROC) were also used to detect variations in the specificity and sensitivity of the tests for various values of the observed thresholds (Hosmer and Lemeshow, 2000; Saveland and Neuenschwander, 1990). Thus, the area under a ROC curve acts as a measure of discrimination or as a measure of the test’s ability to classify live and

Table I. Number of selected PSP for each species by number of measurements.

Species	Number of measurements				Total
	2	3	4	5	
Tolerant* conifers					
Black spruce	504	274	56	5	839
Balsam fir	340	100	48	2	490
Intolerant* conifer					
Jack pine	124	28	10	1	163
Intolerant* hardwoods					
Trembling aspen	57	16	3	0	76
White birch	77	30	14	0	121

* Tolerance classes from Baker, 1949.

dead trees. The test provides a c statistic, which can be interpreted as follows:

$$c = \begin{cases} 0.5, & \text{this result suggests that there is no discrimination,} \\ & \text{i.e. flipping a coin could also predict the event} \\ 0.7 \leq \text{ROC} < 0.8, & \text{ROC value} = \text{"acceptable"} \\ 0.8 \leq \text{ROC} < 0.9, & \text{ROC value} = \text{"excellent"} \\ \text{ROC} \geq 0.9, & \text{outstanding discrimination.} \end{cases}$$

3. RESULTS

After some preliminary tests, the fact of taking into account three random effects caused convergence problems that required simplifications of the model. As a consequence, only the plot effect was considered. This random effect was significant for all species. The number of plot measurements retained by species based on the selection criteria are shown in Table I. Black spruce is the species most represented in the data set with 839 plots, followed by balsam fir (490), jack pine (163), white birch (121) and trembling aspen (76). Descriptive statistics of the permanent sample plots retained at their first measurement are shown in Tables II and III. The average values for all species confounded ranged from 854–1295 stems ha^{-1} for density, 15.4–24.3 $\text{m}^2 \text{ha}^{-1}$ for basal area, 13.5–15.8 cm for quadratic mean diameter, and 8.8–10.2 years for periodicity of remeasurement (Tab. II). The average values for site trees of all species confounded ranged from 10.5–15.8 m for height and 13.7–23.2 cm for quadratic mean diameter (Tab. III).

Results from the tests on fixed effects parameters, estimates of fixed effects and C statistics for the fitted model using GLIMMIX are shown in Tables IV and V. Results for all species revealed significant differences in terms of ten-year mortality rates depending on the species and the method. For black spruce, the method 4+ had a higher ten-year mortality rate (10.0%) when compared to method C (8.7%, $p = 0.0130$), but the former method was found not statistically different with method CD (9.1%, $p = 0.0903$). For balsam fir, the

method 4+ had higher ten-year mortality rate (22.4%) when compared to the two other methods (17.7% ($p < 0.0001$) and 19.0% ($p = 0.0015$), Tab. IV). Removing the effect of the spruce budworm in the PSP database resulted in similar results for black spruce (Tab. V), i.e. the method 4+ had a higher ten-year mortality rate (10.5%) when compared to the two other methods (8.2% ($p = 0.0003$) and 8.6% ($p = 0.0036$)). For balsam fir, the method 4+ also still had a higher ten-year mortality rate for balsam fir (16.3%) when compared to the two other methods (10.4% ($p < 0.0001$) and 10.6% ($p < 0.0001$), Tab. V). However, the mortality rates for this species were lower by 6–8% approximately when compared to PSP that included the effect of the spruce budworm (Tabs. IV and V).

For jack pine, no differences between methods were found for stands with low basal areas (Q1, $\sim 8.2 \text{ m}^2 \text{ha}^{-1}$; Tab. IV). However, the method 4+ based on top height trees had a lower ten-year mortality rate (3.0%) when compared to the two other methods (4.8% ($p = 0.0418$) and 5.2% ($p = 0.0159$)) for plots with medium stand basal areas (median $\sim 14.2 \text{ m}^2 \text{ha}^{-1}$). A similar result was found for plots with high stand basal areas (Q3, $\sim 22.9 \text{ m}^2 \text{ha}^{-1}$), i.e. the method 4+ had a lower ten-year mortality rate (2.9%) when compared to the two other methods (8.4% ($p < 0.0001$) and 9.1% ($p < 0.0001$)). For trembling aspen the method 4+ had also lower ten-year mortality rates (11.9%) when compared to the two other methods (17.7% ($p = 0.0157$) and 19.4% ($p = 0.0026$)). For white birch, no significant differences ($p = 0.056$) were found between methods: the method 4+ had a ten-year mortality rate of 6.4% compared to 8.9% for methods C and CD.

Overall, the highest ten-year mortality rate was found with balsam fir (22.4%, method 4+) whereas the lowest ten-year mortality rate was found with jack pine (2.9% for Q3, method 4+, Tab. IV). The models were excellent in classifying the mortality of the trees, as indicated by the high c statistic values (ROC curves) which ranged from 0.83 to 0.89 (Tab. IV).

4. DISCUSSION AND CONCLUSION

The mortality rates for black spruce and jack pine in this study are in line with those of Raulier et al. (2003) who estimated the ten-year mortality rates of dominant trees for black spruce and jack pine at 8.0% and 2.6%, respectively. Overall, our results did not show clear evidence of lower mortality rates for top height trees using data from permanent sample plots covering tree species of different shade tolerances growing in Québec. Instead we found that depending on the species, top height trees have lower mortality rates (trembling aspen, jack pine with medium and high stand basal areas), higher mortality rates (black spruce and balsam fir) or equal mortality rates (white birch) than codominant trees or codominant and dominant trees combined. The testing hypothesis was thus rejected for three out of five species, of which two (black spruce, balsam fir) are considered shade tolerant tree species (Baker, 1949).

The reasons for this are very likely multifaceted. Tree mortality is a complex and gradual process that often involves multiple interacting contributors (Franklin et al., 1987). At

Table II. Descriptive statistics (mean \pm S.D.)** of the permanent sample plot data (first measurement).

Species	No. of plots	Density (trees ha ⁻¹)		Basal area (m ² ha ⁻¹)		Quadratic mean diameter (cm)		Mean length of period (years)	
Black spruce	839	1035 \pm 522	(100, 3025)	15.4 \pm 8.8	(0.7, 45.5)	13.5 \pm 2.1	(9.3, 21.7)	9.9 \pm 2.7	(4.1, 23.9)
Balsam fir	490	1295 \pm 588	(150, 3975)	24.3 \pm 10.1	(1.2, 56.4)	15.8 \pm 3.2	(10.3, 28.5)	9.1 \pm 2.7	(4.0, 16.0)
Jack pine	163	1026 \pm 553	(125, 2675)	15.5 \pm 9.4	(1.2, 37.0)	13.6 \pm 2.7	(10.0, 22.8)	8.8 \pm 2.0	(4.6, 15.0)
Trembling aspen	76	1008 \pm 507	(125, 2250)	18.9 \pm 10.5	(1.0, 49.5)	15.4 \pm 3.4	(10.0, 26.0)	9.0 \pm 2.4	(4.5, 17.6)
White birch	121	854 \pm 410	(175, 2050)	16.0 \pm 7.7	(1.5, 36.4)	15.6 \pm 3.1	(10.3, 28.1)	10.2 \pm 2.1	(4.8, 15.9)

* S.D. = standard deviation; values in parentheses indicate the range (minimum, maximum).

Table III. Average site tree height and quadratic mean diameter by method* (mean \pm S.D.)** of the permanent sample plot data (first measurement).

Species	Method	No. of trees***	Height (m)		No. of trees	Quadratic mean diameter (cm)	
Black spruce	4+	739	11.8 \pm 3.4	(5.2, 25.3)	3356	18.8 \pm 12.9	(9.1, 39.1)
	C	3356	10.5 \pm 2.8	(4.6, 23.8)	3356	13.7 \pm 9.9	(9.1, 31.5)
	CD	3356	10.7 \pm 2.9	(4.6, 25.3)	3356	14.0 \pm 10.4	(9.1, 34.7)
Balsam fir	4+	419	13.6 \pm 3.4	(4.8, 24.4)	1960	23.2 \pm 16.7	(9.3, 48.9)
	C	1960	11.7 \pm 2.9	(4.8, 21.3)	1960	16.4 \pm 13.0	(9.1, 40.8)
	CD	1960	11.9 \pm 3.1	(4.8, 22.9)	1960	16.9 \pm 13.7	(9.1, 41.2)
Jack pine	4+	143	11.3 \pm 3.8	(5.8, 22.6)	652	18.5 \pm 13.4	(9.4, 33.2)
	C	652	12.4 \pm 3.7	(5.2, 24.0)	652	14.2 \pm 11.1	(9.1, 28.7)
	CD	652	12.5 \pm 3.7	(5.5, 24.0)	652	14.4 \pm 11.4	(9.1, 32.4)
Trembling aspen	4+	89	15.8 \pm 4.8	(6.8, 26.2)	304	22.7 \pm 18.4	(9.3, 43.8)
	C	304	15.3 \pm 3.9	(6.8, 27.1)	304	16.8 \pm 14.7	(9.1, 37.8)
	CD	304	15.3 \pm 3.9	(7.1, 27.1)	304	17.0 \pm 15.3	(9.1, 43.8)
White birch	4+	170	13.8 \pm 4.0	(6.5, 24.8)	484	21.3 \pm 15.2	(9.7, 38.7)
	C	484	12.9 \pm 3.3	(6.1, 24.8)	484	16.4 \pm 13.6	(9.1, 37.9)
	CD	484	13.0 \pm 3.3	(6.1, 24.4)	484	16.6 \pm 13.8	(9.1, 37.9)

* Site tree selection based on the four largest diameter (D_{130}) trees (4+), randomly selecting four trees among those belonging to the codominant cohort (C) or randomly selecting four trees among those belonging to the codominant or dominant cohort (CD).

** S.D. = standard deviation; values in parentheses indicate the range (minimum, maximum).

*** The number of trees for method 4+ is smaller compared to method C or CD because the height of top height trees is not systematically measured in PSP.

the stand level for instance, many biotic and abiotic factors may interact together to contribute to the mortality of trees (Brandt et al., 2003; Hogg et al., 2002). Biotic factors such as spruce budworm epidemics could have been a major contributor to the higher mortality rate of top height trees of balsam fir and black spruce. Indeed, the province of Québec experienced a severe spruce budworm outbreak during the last decades (1974–1990), a period that coincided with the establishment of the PSP network in the province of Québec. The fact that balsam fir top height trees experienced the highest ten-year mortality rate (22.4%) of all species and methods tested is very likely linked to the spruce budworm which is known to severely attack, reduce diameter growth and kill trees during strong outbreaks (Archambault and Beaulieu, 1985; Belyea, 1952; Blais, 1958; Erdle and MacLean, 1999; MacLean, 1984; Pothier and Mailly, 2006). Indeed, when PSPs affected by the spruce budworm were removed from the dataset, the ten-year mortality rate of balsam fir top height trees dropped to 16.3%.

Surprisingly, even after PSPs affected by the spruce budworm were removed from the dataset, balsam fir top height trees still experienced significantly higher mortality rates when compared to codominants or a combination of codominant and dominant trees. Yet, it is been reported that dominant trees severely defoliated and top-killed by the western spruce budworm (*Choristoneura occidentalis* Freeman) do not necessarily die: some trees are able to produce adventitious foliage throughout the length of the crown, allowing them to survive (Fellin and Dewey, 1982). In our study, it appears that the eastern spruce budworm did not precipitate the mortality rate of any particular site tree cohort for these two species, a result which is in agreement with MacLean and Ostaff (1989) who reported that, in the long run, balsam fir mortality due to the spruce budworm is evenly distributed among different sized trees. As a consequence, other factors than spruce budworm epidemics must be invoked to explain the differences in the ten-year mortality rates between selection methods for site

Table IV. *F* tests, estimates for the fixed effect and C statistics for the fitted model using GLIMMIX.

Species	Test on the fixed effect*				Level of basal area (m ² ha ⁻¹)	10-year mortality rate (%) by method**			C statistic
	Effect	D.F.	<i>F</i>	<i>P</i> > <i>F</i>		4+	C	CD	
Black spruce	Method	12785	4.15	0.0385	–	10.0 a (0.5)	8.7 b (0.5)	9.1 ab (0.5)	0.83
Balsam fir	Method	7205	10.90	< 0.0001	Mean (BA = 15.6)	22.4 a (1.4)	17.7 b (1.1)	19.0 b (1.2)	0.86
	Basal area per ha	7205	8.51	0.0035					
Jack pine	Method × basal area per ha	2367	4.70	0.0092	Q1 (BA = 8.2)	3.1 a (0.8)	3.5 a (0.8)	3.2 a (0.8)	0.89
					Median (BA = 14.2)	3.0 a (0.6)	5.2 b (0.9)	4.8 b (0.9)	
					Q3 (BA = 22.9)	2.9 a (0.8)	9.1 b (1.5)	8.4 b (1.4)	
Trembling aspen	Method	1058	4.89	0.0077	–	11.9 a (2.3)	19.4 b (3.3)	17.7 b (3.1)	0.87
White birch	Method	1967	2.88	0.0562	Mean (BA = 17.3)	6.4 a (1.1)	9.0 a (1.4)	8.9 a (1.4)	0.86
	Basal area per ha	1967	3.65	0.0002					

* Method (4+, CD, C).

** Estimates (± standard error) for the fixed effect: for each species, methods with different letters are significantly different ($\alpha = 0.05$).**Table V.** *F* tests, estimates for the fixed effect and C statistics for the fitted model using GLIMMIX for balsam fir and black spruce stands not affected by the spruce budworm.

Species*	Test on the fixed effect**				Level of basal area (m ² ha ⁻¹)	10-year mortality rate (%) by method***			C statistic
	Effect	D.F.	<i>F</i>	<i>P</i> > <i>F</i>		4+	C	CD	
Black spruce (<i>n</i> = 623)	Method	8896	7.65	0.0005	–	10.5 a (0.6)	8.2 b (0.5)	8.6 b (0.6)	0.83
Balsam fir (<i>n</i> = 236)	Method	2905	12.27	< 0.0001	(BA = 26.1)	16.3 a (1.4)	10.4 b (1.1)	10.6 b (1.2)	0.87
	Basal area per ha	2905	11.97	0.0005					

* Number in brackets is the number of permanent sample plots.

** Method (4+, CD, C).

*** Estimates (± standard error) for the fixed effect: for each species, methods with different letters are significantly different ($\alpha = 0.05$).

trees for these two species. There is no clear explanation for these findings, but we can speculate that some veteran trees of these species might have been misclassified as dominant trees or that the top height trees used in this study and identified as live standing trees (state code 10), did not have all the necessary attributes for qualifying as good site trees and died prematurely. Live blowdown trees (state code 12) were rarely present in the data set (data not shown) so the presence of such trees is very likely not responsible for the lower mortality rates found for some methods. Differences in tree physiological processes among the species studied may have played a role in the results observed. It is indeed reported in the literature that taller trees are known to differ physiologically from shorter, younger trees (Ryan et al., 2006). This aspect, however, was beyond the scope of our study and thus was not tested. Finally, the size of the PSPs used in Québec (0.04 ha) may not be large enough to adequately capture the mortality rates as

intended for modelling purposes: small plots may indeed give inaccurate and often biased estimates of mortality (Curtis and Marshall, 2005).

Interestingly, the testing hypothesis was accepted for jack pine (at medium and high stand basal areas) and trembling aspen, both of which are considered shade intolerant species (Baker, 1949). Similar results were found for white birch, i.e. the method 4+ had lower ten-year mortality rates (6.4%) when compared to the two other methods (8.9%), although the differences were not significant ($p = 0.056$). Overall, these results are in opposition to Zeide's assumption that site trees of tolerant species suffer less mortality than those of intolerant species (Zeide, 1981). We hypothesize that the lower mortality rate could be attributable to the fact that top height trees of these shade intolerant species can maintain height dominance during stand development due to faster diameter growth and larger crowns. In the case of jack pine

however this phenomenon appears to happen especially in stands with medium and high basal areas (Tab. IV), suggesting that codominant trees are more prone to die with increasing age and/or stand density. Conversely, the risk associated with tree mortality for subcanopy trees can be exacerbated by shade-induced stress, sometimes associated with the inability of shade intolerant species to maintain viable growth rates under high competition and dense canopy conditions (Lin et al., 2001; Waring, 1987).

Our data do not support unanimously the hypothesis that the mortality rate of top height trees is lower than the mortality rate of codominants only or a combination of codominant and dominant trees. The question of stability of dominance and mortality rates of top height trees in a forest stand in relation with site quality estimates do not appear to pose a major problem with shade intolerant species. With shade tolerant species, however, it appears that using codominants or a combination of codominant and dominant trees results in significantly lower mortality rates. Finally, although the mortality model used in this study worked well with all tree species considered, we feel that a few words of caution are necessary. One drawback to the dataset used in this study was that the majority of the PSP retained based on the selection criteria were measured three times or less. It is possible that the results may have been different if PSP covering a longer time span would have been used. Consequently, we suggest that this study be replicated in other forest ecosystems or geographical areas and with PSP data spanning several measurements to confirm our findings.

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APPENDIX

Table A.1. List of codes used for characterizing the state of merchantable trees in a sample plot*.

State	Code
Live standing tree	10
Live blowdown tree	12
Dead standing tree	14
Snag	16
Missing tree	23
Missing tree or snag	24
Intruder	25
Cut tree	26
Unidentified tree or joined trees	29
Live standing tree, forgotten	30
Live blowdown tree, forgotten	32
Dead standing tree, forgotten	34
Snag, forgotten	36
Live standing recruit	40
Live recruit blowdown	42
Dead standing recruit	44
Snag recruit	46
Live standing tree, renumbered	50
Live tree blowdown, renumbered	52
Dead standing tree, renumbered	54
Snag, renumbered	56

* *Ministère des Ressources naturelles du Québec (2001)*.